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REVIEW OF *LYGOCORIDES* YASUNAGA (HETEROPTERA: MIRIDAE) *

Yasunaga, T., 1996. Review of *Lygocorides* Yasunaga (Heteroptera: Miridae). – Tijdschrift voor Entomologie 139: 267-275, figs. 1-23. [ISSN 0040-7496]. Published 18 December 1996. *Lygocorides* Yasunaga, 1991, proposed as a subgenus of the genus *Lygocoris* Reuter, is upgraded to the generic level, and redefined as a distinctive monophyletic group, based on the conspicuously elongate intertamal lobes of the female genitalia. Two additional species, *L. izjaslavi* from the Primorskij Kraj, Russia and *L. rubricans* from Taiwan and the Ryukyus, Japan, are described. A new subgenus, *Ryukyulygus*, is proposed to accommodate *rubricans*. *Lygocorides rubronasutus* (Linnavuori) is transferred from *Lygocoris*, and diagnosed with description of the last-instar nymph. The zoogeography and phylogeny of the genus are discussed, based on the distributional records and host preference of each species.

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Key words. - Heteroptera; Miridae; *Lygocorides;* new subgenus; new species; Japan; Taiwan; Russian Far East.

Linnavuori (1961) described Lygus rubronasutus from Hokkaido, northern Japan. Subsequently, Miyamoto (1965) placed it in the subgenus Neolygus of the genus Lygus (= Lygocoris Reuter, 1875, not Lygus Hahn sensu stricto; see Carvalho et al. 1961 and China 1963). Kerzhner (1988a, b) recorded this species as Lygocoris (Neolygus) rubronasutus from the southern Primorskij Kraj of the Continental Russian Far East, while Yasunaga (1991) proposed a new subgenus, Lygocorides, to accommodate it, because the male genital structure significantly differs from those exhibited in Neolygus and other known subgenera of Lygocoris.

However, I recently examined both male and female genitalia more closely, and became aware that *Lygocorides* had better be regarded as a distinctive genus. I also had an opportunity to examine several specimens from the Primorskij Kraj, identified as *rubronasutus* by Kerzhner, and recognized that they are not conspecific with Japanese ones. In addition, a third, undescribed species, which in general appearance resembles *rubronasutus*, has been found in good number in the Ryukyus, southern Japan and Taiwan.

In the present paper, *Lygocorides* is redefined as a monophyletic genus. The type species of the genus, *L. rubronasutus*, is also diagnosed, and its last-instar nymph is described and figured. Two additional

species, *L. izjaslavi and L. rubricans*, are described. Since *rubricans* is found to differ sufficiently from *rubronasutus* in the structure of the male and female genitalia, a new subgenus, *Ryukyulygus*, is proposed to accommodate it properly. The zoogeography and phylogeny of the genus are discussed.

All measurements in the text are given in millimeters. Terminology of the male and female genitalia mainly follows Kelton (1955) and Yasunaga (1991). Depositories of specimens examined are abbreviated as follows: Biological Laboratory, Hokkaido University of Education, Sapporo: (HUES); Mr. Ichita's personal collection, Kuroishi, Aomori: (IC); Dr. Miyamoto's personal collection, Fukuoka: (MC); Department of Zoology, National Science Museum, Tokyo: (NSMT); Zoological Institute, Russian Academy of Sciences, St. Petersburg: (ZMAS).

SYSTEMATIC PART

Lygocorides Yasunaga stat. n.

Lygocoris (Lygocorides) Yasunaga, 1991: 446. Type species: Lygus rubronasutus Linnavuori, 1961, monotypic. – Yasunaga 1992a: 528; 1992b: 18, 20. Lygocoris (Lygocoroides) [sic!]. - Schuh 1995: 793.

^{*} Contribution from the Russia/Japan Cooperative East Asian Entomological Program, No. 46.

Redescription

Body subovate, moderate in size, brownish or reddish in general coloration; dorsal surface shining, clothed with silky pubescence. Head vertical, sparsely with erect, short, silky hairs; eye almost contiguous to pronotal collar; vertex smooth, lacking basal transverse carina. Antenna slender; segment I shorter than width of head including eyes; segment II longer than basal width of pronotum, slightly incrassate toward apex; segments III and IV filiform. Rostrum reaching hind coxa.

Pronotum shining, sparsely and minutely punctate, covered with suberect silky pubescence; collar comparatively thick, about as broad as apex of antennal segment II. Scutellum rather flat, weakly shagreened, clothed with suberect silky pubescence. Hemelytra irregularly and finely punctate, densely clothed with silky pubescence, obliquely declivous at cuneal fracture. Hind femur with several long trichobothria; tibial spines pale; tarsomere I shortest; tarsomere II about as long as tarsomere III.

Male genitalia (figs. 3-13). – Right paramere straight, with broad sensory lobe and small pointed hypophysis. Sensory lobe of left paramere noticeably widened, with subbasal protuberance; hypophysis rather short. Vesica with two apical elongate sclerites (= apical sclerites I and II), ventrally hooked gonoporal sclerite and spinulate basal selerite; gonopore thick

rimmed; ejaculatory duct somewhat expanded apically.

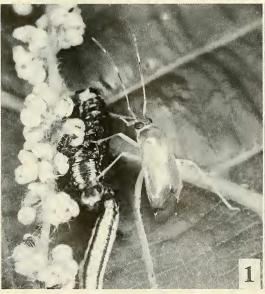
Female genitalia (figs. 14-19). – Selerotized rings subovate, removed mesally one another. Posterior wall of bursa copulatrix with considerably elongate and minutely spinulate interramal lobes; interramal scterite v-shaped, divided mesad; dorsal structure projected and curved.

Discussion

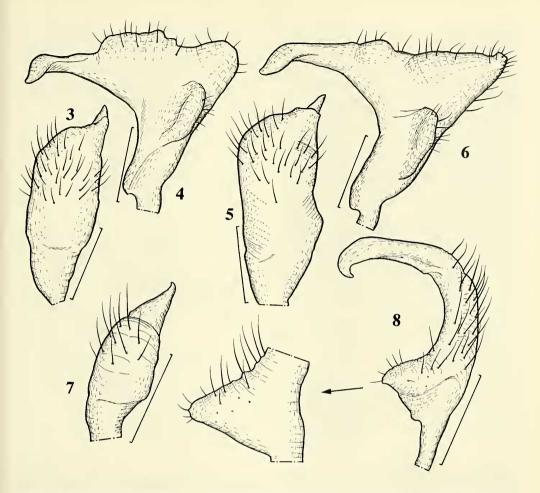
Lygocorides and Lygocoris exhibit similarity in external appearance, but the former is sufficiently different from the latter in the structure of the male and female genitalia, such as the remarkably widened sensory lobe of the left paramere, two noticeable apical sclerites and developed gonoporal selerite presenting on the vesica, smaller selerotized rings, that are not contiguous mesally, and very long interramal lobe and projected dorsal structure of the posterior wall of bursa copulatrix. Especially, the extremely long interramal lobes of the female genitalia, that is considered as a distinct autapomorphy of Lygocorides, is never found in any subgenera of Lygocorides and any related genera (see figs. 17-19). Thus, Lygocorides should be regarded as a distinctive monophyletic genus.

Lygocorides is known by three oak-inhabiting species occurring in the eastern Asia.

Figs. 1-2. Lygocorides rubronasutus on the host plant, Quercus dentata. - 1, male adult sucking on a lepidopteran larva; 2, last-instar nymph.







Figs. 3-8. Parameres of Lygocorides spp. – 3-4, L. rubronasutus; 5-6, L. izjaslavi; 7-8, L. rubricans. – 3, 5 & 7, right paramere; 4, 6 & 8, left paramere. Scales: 0.2 mm.

Lygocorides rubronasutus (Linnavuori) comb. n. (figs. 1-4, 9, 14, 17, 23)

Lygus rubronasutus Linnavuori, 1961: 158.

Lygus (Neolygus) rubronasutus. – Miyamoto 1965: 100, pl. 50; Miyamoto & Yasunaga 1989: 160.

Lygocoris (Lygocorides) rubronasutus. – Yasunaga 1991: 446; 1992b: 20; Yasunaga et al. 1993: 152, pl. 12.

Lygocoris (Lygocoroides) rubronasutus [sic !]. – Schuh 1995: 803.

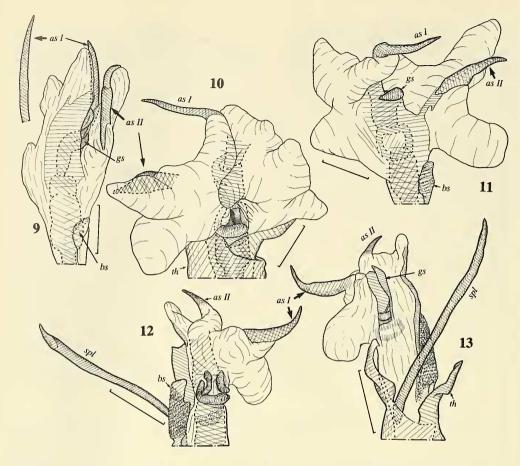
Diagnosis of adult (fig. 1).

Recognized by the shiny brownish general coloration with reddish tinge, dark reddish brown tylus and apex of the cuneus, and characters as mentioned in generic redescription. Detailed redescription including male genital structure was provided by Yasunaga (1991).

Male genitalia. – Parameres as in figures 3-4. Vesical basal sclerite weak, not strongly sclerotized; ventral projection of gonoporal sclerite weak; apical sclerite II with hooked apex(fig. 9).

Female genitalia. – Sclerotized ring comparatively small (fig. 14). Posterior wall of bursa copulatrix relatively narrow, with rather widened interramal sclerites (fig. 17).

Dimensions. $-\delta$ ($\+$): Body length 4.85-5.75 (5.90-6.40), head width 1.09-1.18 (1.18-1.20), length of antennal segment I 0.75-0.95 (0.85-0.95), II 1.95-2.40 (2.25-2.35), III 1.08-1.23 (1.18-1.25), IV 0.74-0.75 (0.75-0.85), rostral length 2.25-2.43 (2.33-2.45), mesal pronotal length incl. collar 1.08-1.25 (1.25-1.28), basal pronotal width 1.83-2.00 (2.03-2.05), length of hind femur 2.20-2.25 (2.20-1.28).



Figs. 9-13. Vesicae of Lygocorides spp. -9, L. rubronasutus; 10-11, L. izjaslavi; 12-13, L. rubricans. -9, 11 & 13, ventral view; 10 & 12, dorsal view. Scales: 0.2 mm. Abbreviations: as I = apical sclerite 1; as II = apical sclerite II; bs = basal sclerite; gs = gonoporal sclerite; th = theca.

2.25), tibia 3.03-3.37 (3.30-3.33), tarsus 0.58-0.68 (0.68-0.70) and width across hemelytra 2.30-2.50 (2.68-2.70).

Material examined. – Japan: [Hokkaido] 1\$\delta\$, Ikeda, Tokachi, on Quercus dentata, 2.vii.1958, S. Miyamoto (paratype, MC); 1\$\delta\$, Bannaguro, Ishikari T., nr. Ishikari Bay, on Q. dentata, 25.v.1996 (first-instar nymph when collected and emerging on 8.vi.), A. Hiranuma (HUES); 1\$\delta\$, 2\$\delta\$, same locality, on Q. dentata, 4.vii.1996, T. Yasunaga (HUES). [Honshu] 1\$\delta\$, 1\$\delta\$, Hiratakinuma, Kizukuri-machi, Aomori Pref., 16.vii.1988, T. Ichita (IC); 2\$\delta\$, 3\$\delta\$, Mt. Kakezu, Geihoku, Hiroshima Pref., on Q. dentata, T. Yasunaga (HUES); 1\$\delta\$, Chojabaru, Geihoku T., Hiroshima Pref., 10-11.vii.1994, light trap, S. Yoshizawa (HUES).

Description of last-instar nymph (fig. 2)

Body oblong-oval; dorsal surface brownish, shining, with sparse vestiture. Head shiny pale brown, partly sanguineous, with reddish brown inner margin of eye, sparsely clothed with erect setae; vertex and frons widely and symmetrically reddish chestnut brown; tylus entirely shiny chestnut brown. Antenna yellowish brown, generally covered with brown suberect setae; segment I provided with several dark erect bristles; apical 1/3 of segment II, apical half of segment III and segment IV except extreme base dark reddish brown; lengths of segments I-IV: 0.54, 1.29, 0.98 and 0.75. Rostrum pale brown, reaching middle coxa; apical half of segment IV darkened.

Pronotum chestnut brown, shining, with yellowish anterior margin and longitudinal mesal stripe, sparse-

ly clothed with suberect short setae, anterolateral and posterolateral angles each with a dark erect spine; thoracic side pale brown, except reddish or brownish ventral half; wing pads shiny dark brown, with pale mesoscutal part, sparsely clothed with short hairs. Legs pale brown, generally clothed with suberect brownish setae; apical part of femur with irregular sanguineous ring and bearing a few dark suberect spines; tibial spines pale brown; apical 1/3 of tarsus darkened; lengths of hind femur, tibia and tarsus: 1.50, 2.25 and 0.52. Abdomen pale red or sanguineous, except pale posterior margin of each segment and darkened segments IX and X, sparsely clothed with indistinct short hairs; dorsal scent gland opening infuscate; apical segments bearing brown setae.

Dimensions. – Body length 4.30, head width 0.98, vertex width 0.48, total rostral length 1.75, pronotal width 1.03, width across wing pads 1.78 and maximum abdominal width 1.95.

Material examined. – 1 ♂, Bannaguro, Ishikari T., nr. Ishikari Bay, Hokkaido, on flower of *Quercus dentata*, first-instar when collected on 25.v.1996, last-instar on 3.vi., A. Hiranuma (HUES).

Distribution. – Japan (restricted areas of Hokkaido and Honshu, where *Quercus dentata* grows).

Remarks. – It seems to be associated strictly with *Quercus dentata* (Fagaceae), because no specimens have been collected from any other species of the deciduous *Quercus* (e.g., *Q. mongolica* var. *grosserrata*, *Q. serrata*). Predation on an unidentified lepidopteran larva was observed in the laboratory (fig. 1).

Although the last-instar nymph of this species exhibits reddish or brownish coloration as described above, more immature nymphs (up to 2nd-instar) are almost uniformly pale green.

Lygocorides izjaslavi sp. n. (figs. 5-6, 10-11, 15, 18, 23)

Lygocoris (Neolygus?) rubronasutus. — Kerzhner 1988a: 68. Lygocoris (Neolygus) rubronasutus. — Kerzhner 1988b: 804. Lygocoris (Lygocorides) rubronasutus. — Miyamoto et al. 1994: 248.

Type material. – Holotype: \vec{o} , Rjazanovka, 10 km NE of Sukhanovka, Khasanskij Dist., S. Primorskij Kraj, Russia, 7.vii.1982, I.M. Kerzhner (the data written in Russian, zmas). – Paratypes: $1\vec{o}$, $1\mathbf{P}$, same data as for holotype (zmas); $4\vec{o}$, $2\mathbf{P}$, same locality, light trap, 26-27.vii.1993, T. Yasunaga (HUES).

Description

Body generally brownish, partly tinged with red, oblong-oval in dorsal view; dorsal surface shining, clothed with silky decumbent or suberect pubescence. Head pale reddish brown, shining, sparsely with silky erect short pubescence; vertex 0.37-0.38 times as wide as head including eyes in 3.0.39-0.42 in 3.0.

Pronotum shiny pale brown, with reddish calli, shallowly and finely punctate, uniformly clothed with silky suberect pubescence, basal margin narrowly carinate; collar yellowish, about as broad as apex of antennal segment II, bearing several brownish erect setae. Scutellum flat, weakly rugose. Ostiolar peritreme yellow. Hemelytra pale brown, somewhat tinged with red, shallowly and irregularly punctate, densely covered with silky decumbent pubescence, not strongly declivous at cuneal fracture; anal ridge and apical 1/3 of cuneus darkened. Leg pale brown; hind femur with one or two obscure rings apically; tibial spines brown; tarsomere III infuscate; length of hind femur, tibia and tarsus: 2.30-2.43, 3.45-3.50 and 0.69-0.75 in δ , 2.27-2.53, 3.45-3.73 and 0.70-0.75 in ♀; that of hind tarsomeres I-III: 0.21-0.25, 0.31-0.36 and 0.29-0.33 in δ , 0.24-0.25, 0.33-0.39 and 0.31-0.36 in \circ . Abdomen pale brown to brown, in 3 with darkened parameres.

Male genitalia. – Parameres as in figures 5-6. Right paramere with ventromedially and triangularly produced sensory lobe and tapered, small hypophysis (fig. 5); left paramere with a strongly projected apical protuberance and rather long hypophysis (fig. 6). Vesical basal sclerite distinct; gonoporal sclerite with a noticeable ventral hook; apical sclerite II with broad base, gradually tapered apically (figs. 10-11).

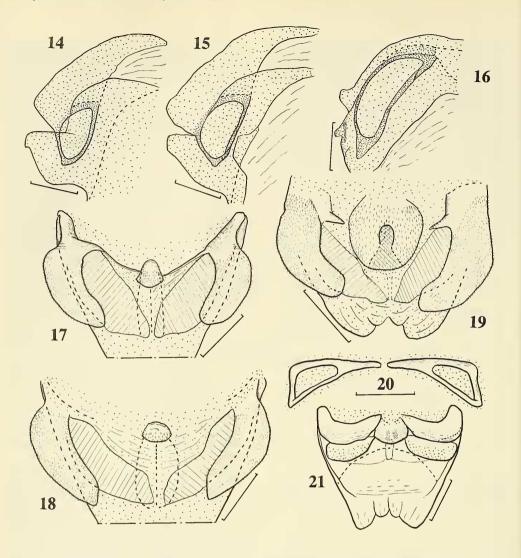
Female genitalia. – Selerotized ring oval (fig. 15). Posterior wall of bursa copulatrix wide, with elongate interramal lobes and narrow interramal selerite (fig. 18).

Dimensions. δ (\mathfrak{P}): Body length 5.60-6.45 (6.00-6.70), head width 1.14-1.19 (1.15-1.21), rostral length 2.40-2.50 (2.50-2.68), mesal pronotal length incl. collar 1.25-1.30 (1.23-1.32), basal pronotal width 2.00-2.09 (2.01-2.20), and width across hemelytra 2.50-2.63 (2.49-2.83).

Etymology. – Named after Dr. Izjaslav M. Kerzhner, who first collected this species.

Distribution. – Continental Russian Far East (southern Primorskij District).

Remarks. - Kerzhner (1988a, b) and Miyamoto et al. (1994) regarded the specimens from the



Figs. 14-21. Female genitalia of *Lygocorides* spp. (14-19) and *Lygocoris pabulinus* (type species of *Lygocoris*, 20-21). – 14 & 17, *L. rubronasutus*, 15 & 18, *L. izjaslavi*; 16 & 19, *L. rubricans*. – 14-16 & 20, sclerotized ring; 17-19 & 21, posterior wall of bursa copulatrix. Scales: 0.2 mm.

Continental Russian Far East to be conspecific with *rubronasutus* of Japan. But they have the following features different from Japanese *rubronasutus*: the generally larger size, wider vertex, longer antennal segment III that is longer than the mesal pronotum including collar, and different structure of the male and female genitalia.

Kerzhner (1988b) recognized *Quercus dentata* as its host plant.

Ryukyulygus subgen. n.

Type species. – *Lygocorides rubricans* Yasunaga, new species.

Description

Almost similar in general appearance to *Lygocorides* s. str., but differing in the following characters: body more oval; vertex with weak, but visible basal transverse carina; antenna generally shorter; hemelytra strongly declivous at cuneal fracture; hind tarsomere III longer than I or II; right paramere with long and

basally broadened hypophysis (fig. 7); left paramere not strongly widened, with basally produced sensory lobe; vesica with a distinct spiculum, developed basal sclerite, not ventrally projected gonoporal sclerite and shorter apical selerites (figs. 12-13); theca slender and elongate apicad (fig. 13); female selerotized ring enlarged, elongate-oval (fig. 16); posterior wall of bursa copulatrix with large dorsal structure and widened interramal lobes that are each accompanied with a pointed process at inner base (fig. 19).

Etymology. – Named after the type locality, the Ryukyus, in combination with the generic name *Lygus* Hahn; gender masculine.

Discussion

The present new subgenus and nominotypical subgenus share such characters in the genitalia as the basal sclerite and two apical selerites on the vesica, and spinulate, extremely projected interramal lobes and V-shaped interramal selerite of the posterior wall. But *Ryukyulygus* is readily distinguished by the structures as described above.

Ryukyulygus is represented by a single subtropical species.

Lygocorides (Ryukyulygus) rubricans sp. n. (figs. 7-8, 12-13, 16, 19, 22-23)

Type material. – Holotype: ♂, Mt. Yuwan-dake, Uken vl., Amami-Oshima Is., the Ryukyus, Japan, 29-30.v.1993, T. Yasunaga (HUES). - Paratypes: JAPAN: [Amami-Oshima Is.] 18, Nishinakama, Sumiyo vl., 29.v.1993, Т. Yasunaga (ниеs); 18 д, 5, same data as for holotype (HUES); 2, 3, same locality, 30.v.1993, S. Yoshizawa (HUES); 10, same locality and collector, 21.iv.1996 (HUES); 1∂, 2♀, same locality and collector, 22.iv.1996 (ниеs); 2 д, 29, same locality, 27.v.1996, M. Takai(HUES); 1∂, Akaoki, Tatsugo T., 1.vi.1993, T. Yasunaga (HUES); 13, Mt. Yuidake, Setouchi T., 22.iv.1996, S. Yoshizawa (HUES). [Okinawa Is.] 1♂, 1♀, Yona, Kunigami vl., light trap, 20-25.v.1993, T. Yasunaga (HUES). [Ishigaki Is.] 63, 39, Mt. Banna-dake, 18.iii.1991, M. Owada (NSMT); 1♂, 1♀, Omoto-Takeda, on flowers of evergreen Quercus sp., 24.i.1996, M. Takai (HUES). [Iriomote Is.] 13, Maryudo Waterfall, Urauchi River, 12.iv.1986, T. Yasunaga (HUES); 1♂, Funaura, at light, 11.v.1993, M. Hayashi (HUES); 1♂, 1♀, Mt. Komidake, 23.iv.1981, K. Baba (NSMT); 1♀, Monbanare, nr. Otomi, on flower of Schima wallichii, 13.v.1993, T. Yasunaga (HUES). - TAIWAN: 1♀, Sanping, nr. Liukuei, S. Taiwan, 21-23.vi.1985, M. Miyazaki (NSMT).

Description

Body pale brown to reddish brown, oval; dorsal



Fig. 22. Female of Lygocorides rubricans.

surface shining, uniformly with silky pubescence. Head pale brown, somewhat tinged with red, vertical, with erect pubescence; vertex 0.32-0.35 times as wide as head including eyes in δ , 0.34-0.37 in $\mathfrak P$, with visible basal transverse carina that is obsolete mesally; tylus dark brown. Antennal segment I pale brown; segment II pale brown, with darkened apical part, somewhat incrassate toward apex; segments III and IV dark brown, filiform; basal 3/4 of segment III and extreme base of IV pale brown; length of segments I-IV: 0.78-0.83, 1.96-2.18, 1.02-1.19 and 0.63-0.78 in δ , 0.78-0.88, 2.06-2.33, 1.15-1.38 and 0.73-0.75 in $\mathfrak P$. Rostrum reddish pale brown, reaching hind coxa; apical half of segment IV infuscate.

Pronotum shiny pale brown or reddish brown, finely and sparsely punctate, uniformly clothed with silky suberect pubescence; collar narrower than apex of antennal segment II. Scutellum flat, very weakly shagreened and wrinkled. Hemelytra concolorously pale brown to reddish brown, shallowly and irregularly punctate, uniformly covered with silky pubescence, declivous at cuneal fracture; membrane pale grayish brown, with partly reddish veins. Leg pale reddish brown; hind femur with two sanguineous rings apically; tibial spines pale reddish brown; apex of tarsomere III darkened; length of hind femur, tibia and tarsus: 1.98-2.25, 2.58-3.08 and 0.59-0.65 in 3, 2.05-2.35, 2.83-3.23 and 0.63-0.73 in ♀; that of hind tarsomere I-III: 0.16-0.19, 0.24-0.28 and 0.26-0.31 in δ , 0.20-0.24, 0.26 and 0.29-0.31 in \circ .

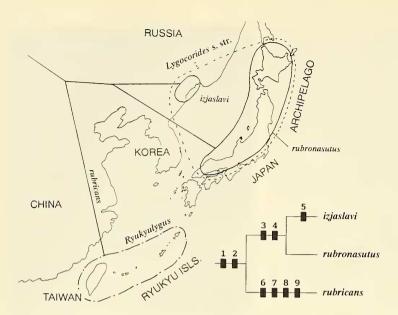


Fig. 23. Distribution map and phylogenetic relationships of *Lygocorides* spp. Numbers of the autand synapomorphics corresponding with those mentioned in the text.

Abdomen pale reddish brown; ventromedian part of male genital segment (pygophore) and parameres widely dark chestnut brown.

Male and female genitalia as mentioned in subgeneric description.

Etymology. – From the Latin, referring to the reddish general coloration.

Distribution. – Japan (the Ryukyus: Amami-Oshima, Okinawa, Ishigaki and Iriomote Isles); Taiwan.

Remarks. – This new species has been found on several evergreen broadleaved trees and flowers of the Saxifragaceae and Theaceae. It is occasionally attracted to light. The only confirmed host plant is evergreen species of *Quercus* (subgen. *Lepidobalanus*), from which several teneral adults were collected.

Zoogeography and Phylogeny (fig. 23)

Aut- and synapomorphies shown in figure 23 are as follows: 1, the interramal lobe conspicuously projected; 2, vesica with a pair of apical sclerites (I and II); 3, left paramere with noticeably widened sensory lobe; 4, gonoporal sclerite with a ventral process; 5, ventral

process of gonoporal sclerite distinct and strongly hooked; 6, vesica with a distinct, long spiculum; 7, basal sclerite of vesica well developed; 8, sclerotized ring enlarged; 9, basal part of interramal lobe with an inner pointed process.

As mentioned in the generic discussion, presence of the extremely projected interramal lobes in the female genitalia is considered as an autapomorphy of the genus Lygocorides (1). In addition, all the species of this genus exhibit great similarity in external appearance and, without exception, are oak-inhabitants. Two species of the nominotypical subgenus are restricted to deciduous Quercus dentata, and L. rubricans is confirmed to be associated with evergreen Quercus. Although Lygocorides is similar to Lygocoris, I conclude that any relationships between the two genera are superficial. For example, the shiny, finely punctate dorsum uniformly provided with a simple vestiture and reduced basal transverse carina of the vertex are not unique to Lygocoris and Lygocorides, but are frequently found in other groups of the tribe Mirini. Any mirine genera confidently related to Lygocorides have not been determined yet. The mirine plant bug fauna of the eastern Eurasia is said to be still in great need of investigation, and a much broader survey on taxa and characters is required to establish the phylogenetic relationships of Lygocorides and other superficially similar mirine genera. I herein discuss only the zoogeography and ingroup phylogeny.

Lygocorides rubronasutus and L. izjaslavi are more closely related one another, and are included in the

nominotypical subgenus, sharing the characters 3-4. They are considered to be derived from a common ancestor occurring in the eastern part of Continental Eurasia. In the Quaternary Ice Age, its population invaded to Japan through the landbridges that connected Japan with the continent. They have been allopatrically speciated from one another since the Japan Archipelago was isolated by the Straits from the Continental Eurasia at the end of the Würm Glaciation. Similar zoogeographical distribution and speciation patterns were indicated in the lycaenid butterflies, Japonica spp., that are also associated with deciduous Quercus (Saigusa 1993).

On the other hand, L. rubricans seems to have been speciated in the eastern Continental Eurasia earlier than rubronasutus and izjaslavi, becoming associated with evergreen species of Quercus, presumably before the Quaternary Ice Age when the climate was even warmer. Then, rubricans spread in the continent, but only the population that invaded the Ryukyu Islands via Taiwan through a landbridge during the Würm Glaciation has survived on evergreen Quercus of these areas. The placement of rubricans in the subgenus Ryukyulygus is supported by the apomorphic states of

characters 6-9.

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